THE HYPOSTASE AND SEED STERILITY IN THE ONAGRACEAE

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Numerous species of the Onagraceae (Oenotheraceae) present a high degree of ovular sterility which is difficult to explain. This is well known to all research workers on the Onagraceae and was forcibly brought to my attention the past year during investigations on Clarkia elegans. It was extremely exasperating to be forced to discard slide after slide which should normally show either mature embryo sacs, syngamic stages or zygotes but which exhibited merely empty embryo sac cavities. The ovaries were taken from pedigree cultures; no seed germination studies have been carried out, but the slides show that sterility is widespread and more than a purely genetical phenomenon.

An attempt was naturally made to ascertain the cause of this extensive embryo sac abortion. It early became apparent that the cause was to be found in physiological rather than genetical disturbances. The most commonly accepted theories to account for ovular sterility were discarded as being incapable of experimental proof.

The ovules of other species of the Onagraceae were examined and compared with those of Clarkia elegans. The investigation had not proceeded far before it was discovered, by personal observation and a review of the literature, that seed sterility was absent in those species which lacked the so-called "hypostase" of van Tieghem. What was previously merely a vague suspicion became a foregone conclusion: there was an intimate connection between the presence of a hypostase and seed sterility.

The hypostase was first described in 1893 by Ph. van Tieghem.[1] He first designated the structure under consideration as the "cupule lignifée." However, it was of such general occurrence and assumed such varied characteristics that a comprehensive name designed to embrace all manifestations was proposed in the name "hypostase." Two other papers by van Tieghem on the hypostase appeared later.[2, 3] Outside of a brief discussion by Ishikawa,[4] the subject has been completely ignored by botanical investigators.

As far as the present note is concerned it is unnecessary to go into a detailed discussion of the hypostase; all that is required is an understanding of what constitutes the hypostase in the ovule of the Onagraceae. Briefly, it consists of a well defined but irregularly outlined group of thick-walled cells at the chalazal end of the ovule, situated directly on top of the end of the vascular bundle entering from the raphe, and which ordinarily but not invariably extends to the base of the embryo sac. The cells are filled with a substance which stains intensely with the usual chromatin stains and with chlorophyll solution. Ishikawa concludes it is an ultimate substance, though he repeatedly and erroneously calls it a "chromatic substance." The hypostase

[1] Bull. de la Soc. Bot. 40: 347. 1893.
[2] Bull. du Mus. d'Hist. Nat., Paris 7: 412-418. 1901.
[3] Ann. Sci. nat. Bot. VIII, 7; 347-362. 1903.
[4] Ann. Bot. 32: 279-317. 1918.

stains so brilliantly that it cannot be overlooked if present. The inner integument is directly continuous with the hypostase. However, there is a sharp distinction between the two; the former is a definite structure while with the latter, indefiniteness of extent is one of its main characteristics. Moreover, the deposition of a substance in the cells of the inner integument occurs whether or not a hypostase is present.

Properly speaking, the hypostase can hardly be called a structural unit of the ovule since the cells without their peculiar contents are indistinguishable from the surrounding cells not a part of the hypostase. Rather, it is a definite portion of the ovule in which the metabolic processes of the entire intraintegumental region are concentrated. That is the only conclusion which the facts permit. The limits of expansion of the hypostase are quite well defined though not structurally delimited at every point.

The hypostase makes its appearance quite early in the life of the ovule — usually just preceding the first meiotic mitosis. It rapidly becomes functional and is the sole arbiter of the destiny of the embryo sac. Its functional balance is presumably very delicate; it appears that once a violent disturbance occurs, recovery is impossible. In ovules possessing a hypostase, all nutritive materials intended for the developing embryo sac must pass through that region. Entrance of these food materials may be effectively blocked by changes in the cells comprising the hypostase, with the consequent death, degenerance and disappearance of the embryo sac previous to syngamy. The nature of the functional disturbances in the hypostase is a moot question; whatever their nature, they are of vital importance in the development of the seed.

The possible causes may be briefly summarized as follows: (1) the cell walls may become so thick as to form an impervious barrier; (2) environmental influences, such as sudden rises in temperature, excessive drought, etc.; (3) temporary stoppage of the food supply to a particular ovlue; (4) some substance inimical to the metabolic function may be formed or deposited in the cells; (5) the stimulation effected by fertilization may be required for the continued functioning of the hypostase; (6) the tendency towards possessing a non-functional hypostase may be dominant and hereditary in some degrees.

In ovules in which the embryo sac had entirely disappeared, presumably thru the non-functioning of the hypostase, one of the most noticeable effects was the abnormal development of those portions of both integuments surrounding the raphe. In many cases there was an astonishing increase in size (often as much as ten times normal size) of the two layers of cells of the outer integument. The obvious explanation is that the food intended for the embryo sac never reached it and was deposited in the integuments with consequent hypertrophy of the latter. Such ovules when matured have about the same size as normal seeds containing embryos, but naturally do not germinate. In other cases the nucellar cells are shrunken and that side of the ovule opposite the raphe is crushed inwards. Among collected seeds these

latter constitute the powdery "seed-like structures" mentioned so often by Davis and other workers on Oenothera.

Oenothera, Gaura, Clarkia, Eucharidium and Circaea possess definite hypostases, while Ludwigia, Jussiaea, Godetia and the majority of species of Epilobium and Fuchsia are characterized by its absence. The first group is notorious for the presence of tiny, malformed seeds incapable of germination, while such are practically unknown in the latter group. For Zauschneria, Lopezia and Boisduvalia, there is no data regarding the presence or absence of hypostases; all three are said to have wholly fertile seeds, hence one may conclude that these lack a hypostase.

In conclusion the author holds that germination tests of seeds of species of the Onagraceae possessing a hypostase in their ovules are of no significance or value whatever, for reasons which are so obvious that they need not be elaborated.

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THE BOTANICAL EXPLORERS OF CALIFORNIA.—I.

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Definite botanical exploration of California has been proceeding for something like one hundred and forty years. More or less of the field work of the earlier explorers has been made a matter of printed record. The interval of the last fifty years covers a period represented by much devoted field work on the part of certain men who have passed away without mention or with only scant notice. Without exception these collectors contributed results of their field studies and material from their collections unstintedly and widely, more especially to those engaged on major botanical tasks. It has appeared, therefore, unfitting that the men who had in this way done much to promote the progress of systematic botany in California and North America should pass on without a word of memorial. It is not difficult for anyone with some gift of expression to write a felicitous appreciation of personality and character, and this is well worth doing. However, it has seemed to the writer that a real memorial should rather bring together the essential facts in regard to the life of the explorer and the important information regarding his field work in a permanently accessible form. Research men in systematic botany raise almost endless questions in regard to the field of operation of a botanical collector and his plant materials. A memorial, therefore, which is useful for reference seems the kind worth making. A sound view this, we think, but how difficult to realize! Facts, as is well known, are exceedingly expensive to assemble, and in a given case their assembling may not prove feasible. Information which might readily be had in a collector's lifetime, is lost with his death. When an explorer is no longer living it is often disconcertingly difficult to make a record of his collecting expedi-